



Galls and Phytochemistry: a case study of Myrtaceae superhosts with emphasis on *Neomitranthes obscura*

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ABSTRACT

The Myrtaceae is rich in phenolics and volatile terpenoids and has many reported associations with gall inducers in Brazilian *restinga*. These metabolites protect plants against both biotic and abiotic stresses, but also play a crucial signaling role in plant-herbivore interactions, especially on superhosts like *Neomitranthes obscura*. We hypothesize that the chemical identity of the superhosts relates to their capacity to respond to diverse galling herbivores, which was assessed through a two-step bibliographic survey resulting in 52 analysed documents. The prevalent classes of chemical compounds in the superhost Myrtaceae are hydrocarbonated (SH) and oxygenated sesquiterpenes (OS), which are related to plant identity and its interactions with the galling organisms. Among the superhost Myrtaceae, *Neomitranthes obscura* shares sesquiterpenic and phenolic derivatives with other host plants, which makes it impossible to infer why some species are superhosts while others are not. Our results suggest that a greater diversity of terpenoids may be related to metabolic flexibility, potentially increasing the ability of hosting galling species. However, further research is needed to explore this relationship, particularly in conjunction with other key metabolite classes in Myrtaceae, such as phenolic compounds.

Keywords: Galls, Monoterpenes, Plant-insect interactions, Sesquiterpenes, Terpenoid profile.

Received July 30, 2024; Accepted January 22, 2026

Editor-in-Chief: Thaís Elias Almeida; Associate Editor: Anderson Ferreira Pinto Machado

How to cite:

Ribeiro MAM, Soares GLG, Ferreira BG, Gomes CVC, Arriola IA, Isaías RMS. 2026. Galls and Phytochemistry: a case study of Myrtaceae superhosts with emphasis on *Neomitranthes obscura*. *Acta Botanica Brasilica* 40: e20250135. doi: 10.1590/1677-941X-ABB-2025-0135



Introduction

The secondary metabolites can influence the association of plants with herbivores, such as gall inducers, through both attraction and repellence (Hall *et al.*, 2017; Divekar *et al.*, 2022). For some plant families, such as Myrtaceae, the second-largest family of the Atlantic Forest (Stehmann *et al.*, 2009), the chemical diversity of compounds may be related to the richness and diversity of associated gall inducers (Hall *et al.*, 2017). The diversity of plant-herbivore associations is often linked to host species richness (Maia *et al.*, 2014; Grandez-Rios *et al.*, 2024). Therefore, we focused on the Myrtaceae, one of the most species-rich families in the Brazilian restinga, to study galling herbivore superhosts (Souza & Morim, 2008; Lourenço & Barbosa, 2012; Maia, 2019). The largest and most diverse genera of Myrtaceae in the Neotropical region are *Eugenia* L., *Myrcia* DC., and *Psidium* L. (Mabberley, 1997; Rosario *et al.*, 2005; Martins *et al.*, 2008; Giaretta & Peixoto, 2015; Govaerts *et al.*, 2019), which are also rich in interactions with galling insects (Maia, 2019).

The attractiveness and repellence of these insects may be related to the accumulation of essential oils, steroids, and phenolic compounds, including flavonoids and tannins, which are common in Myrtaceae (Ramirez *et al.*, 2012; Girardelo *et al.*, 2020). Among the chemical classes of lipidic substances in Myrtaceae, terpenes constitute a broad class of metabolites that play a crucial role in plant ecological interactions, particularly in adapting to abiotic and biotic stresses, including associations with herbivores and pathogens (Victório *et al.*, 2018; Toffolatti *et al.*, 2021). Volatile terpenes, such as mono- and sesquiterpenes, can play a prominent role in signaling insect-plant interactions in very specific ways (Holopainen *et al.*, 2013; Naidoo *et al.*, 2018). For example, the concentration of certain monoterpenes determines species selection in Apiaceae by psyllid species (Homoptera: Psyllidae) (Valterová *et al.*, 1997). One example of a complex phenomenon modulated by these substances involves β -caryophyllene, which is produced by the flowers of several plant species and functions as an alarm pheromone for aphids (Holopainen *et al.*, 2013). The volatile compounds produced by galls are also related to the defense of gall-inducers against browsing mammals (Rostás *et al.*, 2013), acting as possible deterrents of the natural enemies of gall inducers. On the other hand, they can be synthesized by host plants and attract parasitoids of the gall inducers, a role yet understudied (Borges, 2018).

The terpenoid profile in Myrtaceae, especially in its most diverse genera – *Myrcia*, *Eugenia*, and *Psidium* (Amorim & Alves, 2012) – reveals a predominance of flavonoids, mono- and sesquiterpenes (Saber *et al.*, 2023; Keszei *et al.*, 2010). The genus *Eugenia* is rich in flavonoids such as quercetin, myricetin, and kaempferol, tannins, chalcones, and monoterpene hydrocarbons such as α -pinene, β -pinene, and linalool (Oliveira AMD *et al.*, 2006; Pino *et al.*, 2005;

Queiroz *et al.*, 2015; Ribeiro *et al.*, 2016; Silva PR *et al.*, 2021). Flavonoids comprise one of the most diverse groups of natural products, with 9,000 different structures discovered to date, and diverse functions, including UV protection and signaling events (Papoutsis *et al.*, 2021). The genus *Myrcia* is also rich in flavonoids such as myricetin, phenolic acids, and sesquiterpene hydrocarbons such as ε -caryophyllene, δ -cadinene, and caryophyllene oxide (Ferreira *et al.*, 2006; Stefanello *et al.*, 2010; Pereira-Júnior, 2018; Araújo *et al.*, 2020). Sesquiterpenes occur as hydrocarbons or in oxygenated forms, including essential oils and aromatic constituents with pharmacological activities, for example (Papoutsis *et al.*, 2021). In several species of *Psidium*, the major compounds identified are sesquiterpene hydrocarbons (Pino *et al.*, 2003; Padovan *et al.*, 2014; Santos *et al.*, 2022). Sesquiterpenes are mostly liquid and are mainly found in the volatile oils of plants, and their oxygen-containing derivatives are also widely found in volatile oils (Yang *et al.*, 2021).

The chemical diversity of Myrtaceae is, in most cases, related to evolutionary factors and abiotic and biotic pressures, such as an arms race against herbivores, including specialists like the gall inducers (Padovan *et al.*, 2014; Maia, 2019; Martins *et al.*, 2023). These plant-insect interactions are responsible for structural and metabolic alterations in host plant cells and tissues, leading to gall development (Oliveira *et al.*, 2016). At the structural level, gall inducers promote changes such as hyperplasia, cell hypertrophy, tissue homogenization, neoformation of vascular tissues, and redifferentiation of specialized tissues at the gall developmental site (Ferreira *et al.*, 2019). Host plants may be associated with one or more inducers, comprising the superhosts (Isaias *et al.*, 2013), which reflect the diversity of morphogenetic pathways and, consequently, changes in the biosynthesis of secondary metabolites (Oliveira DC *et al.*, 2006; Guedes *et al.*, 2016, 2023; Jorge *et al.*, 2018), which are crucial for the understanding of these interactions. In general, phenolic derivatives are strongly associated with plant defenses against oxidative stresses (Isaias *et al.*, 2015) but may also play a crucial role in hormonal regulation (Bedetti *et al.*, 2017; 2018). While free-living herbivores can be harmed by astringent and antinutritional phenolics, the role of these phenolic compounds as signals for oviposition by galling insects has been observed (Roininen *et al.*, 1999), and they can also be detected in gall tissue compartments, such as the nutritive tissue promoting the disponibilization of specific nutrients (Isaias *et al.*, 2018; Arriola *et al.*, 2024; Souza *et al.*, 2024).

As expected, due to the chemical diversity of Myrtaceae, the terpenoid profile of the superhost species can vary in quantity and quality. In *Myrcia splendens* (SW.) DC., there was a decrease in the amount of δ -muurolene, β -elemene, and α -caryophyllene after the removal of *Nexothrips* sp. individuals from leaf-rolling galls (Jorge *et al.*, 2018), indicating the suppression or neo-synthesis of compounds



due to the stimuli of the gall inducers. By investigating the literature on the terpenoid profile of Myrtaceae, which are superhosts of galls in Brazilian *restingas*, we aim to verify if the species have chemical similarities related to their capacity to attract and respond to diverse galling herbivores. Accordingly, we may identify peculiarities related to species-specific gall morphotypes, using as a case study the superhost Myrtaceae *Neomitranthes obscura* (DC.) N.Silveira, which bears six distinct gall morphospecies, is abundant on the sandy coastal plains of Southeast Brazil and is rich in lipophilic terpenoids.

Materials and Methods

The study was carried out in two steps: the first step involved a search for superhost species of Myrtaceae in the *restinga* biome, using Google Scholar from January to June 2025. This search resulted in 16 species: *Eugenia astringens* Cambess., *E. copacabanensis* Kiaersk., *E. hiemalis* Cambess., *E. puniceifolia* (Kunth) DC., *E. speciosa* Cambess., *E. sulcata* Spring ex Mart., *E. uniflora* L., *Myrcia amazonica* DC., *M. brasiliensis* Kiaersk., *M. ovata* Cambess., *M. palustris* DC., *M. splendens* (SW.) DC., *Myrciaria floribunda* (West ex Willdenow) Berg, *Neomitranthes obscura* (DC.) N. Silveira, *Plinia peruviana* (Poir.) Govaerts, and *Psidium cattleianum* Sabine, as reported in Maia (2013) and Maia (2019).

The second step was the association of the species names with the terms “chemical profile”, “phytochemical profile”, and “phytochemical studies”, and the corresponding terms in Portuguese (“*perfis químicos*”, “*perfis fitoquímicos*”, and “*estudos fitoquímicos*”), both in Google Scholar and Web of Science (Fig. 1). The synonyms of *E. astringens*, *E.*

hiemalis, *E. puniceifolia*, *M. amazonica*, *M. brasiliensis*, *M. palustris*, *M. splendens*, *P. peruviana*, and *P. cattleianum* were included in the search (Table 1). The accepted names for the Myrtaceae species were chosen in accordance with Flora e Funga do Brasil (2025). These two steps were summarized in a flowchart (Fig. 1). No time range was applied to the articles, book chapters, dissertations, and theses. An additional step was the analysis of the papers to identify their approaches. We include neither the methodological procedures for metabolite extraction nor the papers with no details of the chemical compounds. The data related to the more abundant secondary metabolites, terpenes, and phenolic compounds were compiled (Table 1).

We used usual biodiversity measures to convert the multiple variables into intuitive and straightforward data (Boulet *et al.*, 2010; Hilker, 2014) to evaluate the diversity profiles of four chemical subclasses (monoterpene hydrocarbons, oxygenated monoterpenes, sesquiterpene hydrocarbons, and oxygenated sesquiterpenes). The diversity index of chemical subclasses (DCQ) was calculated for each chemical class based on its species profile. The DCQ index was calculated by the Shannon-Wiener formula ($-\sum p_i \times \ln p_i$), where p_i represents the richness proportion of a class concerning the total richness of the species (Table 2). As direct biological interpretation is not possible (Jost, 2006), we calculated the true diversity index (DV) from the exponential chemical diversity index (e^{DCQ}). This index quantifies the number of chemical subclasses effectively present in each species, allowing a more intuitive comparison of the magnitude of the differences among species (Chao *et al.*, 2014). The diversity analyses were performed in PAST – Paleontological Statistics Software Package (Hammer *et al.*, 2001). To compare and visualize the distribution

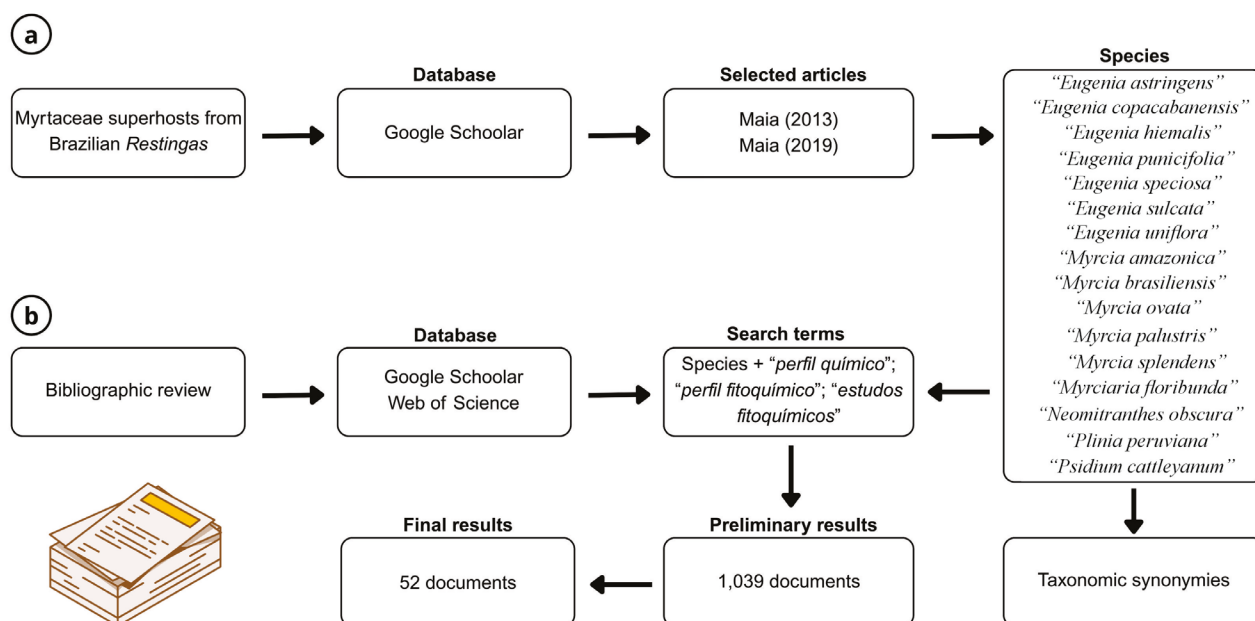


Figure 1. Flowchart of the steps employed in the literature review.



Table 1. Superhost Myrtaceae of Brazilian *restingas* with information on their associated gall inducers, morphotypes, chemical compounds, and biological activity

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Eugenia astringens</i> Cambess. / = <i>E. umbelliflora</i> O. Berg, <i>E. rotundifolia</i> Casar	1. Marginal roll, green, glabrous, one-chambered 2. Bud, cylindrical, brown, glabrous, one-chambered 3. Lenticular, yellow, glabrous, one-chambered 4. Conical 5. Conical. 6. Claviform, reddish, glabrous, one-chambered 7. Stem, fusiform. 8. Globoid, green, glabrous, one-chambered 9. Lenticular, green, glabrous, one-chambered	1. <i>Dasineura marginalis</i> Maia, 2005 (Cecidomyiidae, Diptera) 2. <i>Stephomyia rotundifoliorum</i> Maia, 1993 (Cecidomyiidae) 3. <i>Dasineura globosa</i> Maia, 1995. (Cecidomyiidae) 5. Cecidomyiidae 6. <i>Stephomyia clavata</i> (Tavares 1920) (Cecidomyiidae) 7. Undetermined 8. Undetermined 9. <i>Jorgenseniella eugeniae</i> Maia, 2005 (Cecidomyiidae)	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; caryophyllene oxide; (E)-caryophyllene; β -selinene; α -selinene; γ -cadinene; α -cadinol; globulol; α -copaene; α -cubebene; α -muurolol; limonene; viridiflorene; viridiflorol; aromadendrene	Astringents and Antioxidant activity	Leaves and Buds	–	Apel <i>et al.</i> (2002); Magina <i>et al.</i> (2009); Ramos <i>et al.</i> (2010); Defaveri <i>et al.</i> (2011); Silva TD <i>et al.</i> (2021); Pinto <i>et al.</i> (2022)
<i>Eugenia copacabanensis</i> Kiaersk /-	1. Spiraled, reddish, glabrous, one-chambered. 2. Bud, conical, green, glabrous, pedunculated. 3. Leaf roll, reddish, glabrous, one-chambered. 4. Leaf gall 5. Stem gall 6. Stem gall 7. Fusiform, reddish, glabrous, one-chambered. 8. Conical, reddish, glabrous, one-chambered 9. Lenticular, green, glabrous, one-chambered. 10. Marginal roll, green, glabrous, one-chambered. 11. Globoid, green, glabrous, one-chambered. 12. Bud, rosette, green, glabrous, one-chambered. Galler: Undetermined	1. <i>Stephomyia espiralis</i> Maia, 1993 (Cecidomyiidae) 2. <i>Dasineura copacabanensis</i> Maia, 1993 (Cecidomyiidae) 3. <i>Dasineura</i> sp. (Cecidomyiidae) 4. Cecidomyiidae 5. Cecidomyiidae 6. Hymenoptera 7. <i>Stephomyia tetraloba</i> Maia, 1993 (Cecidomyiidae) 8. <i>Bruggmannia</i> sp. (Cecidomyiidae) 9. Undetermined 10. Undetermined 11. Hymenoptera 12. Undetermined	α -pinene; β -pinene; α -humulene; allo-aromadendrene; caryophyllene oxide; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D; globulol; α -copaene; α -cubebene; α -muurolol; viridiflorol; aromadendrene; γ -elemene	Antioxidant activity	Leaves, buds, and stems	Quercetin	Nakamura <i>et al.</i> (2010); Arruda & Victório (2011); Carvalho-Junior <i>et al.</i> (2014)

Table 1. Cont.

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Eugenia hiemalis</i> Cambess. / = <i>E. hyemalis</i> Cambess.	1. Bud, cylindrical, brown, glabrous, one-chambered. 2. Lenticular, green, glabrous, one-chambered. 3. Marginal roll, green, glabrous, one-chambered. 4. Conical, yellow, glabrous, one-chambered. 5. Claviform, green or reddish, glabrous, one-chambered 6. Conical, yellow, glabrous, one-chambered. Galler: Cecidomyiidae	1. <i>Stephomyia</i> sp. (Cecidomyiidae) 2. Lasiopteridi (Cecidomyiidae) 3. Cecidomyiidae 4. Cecidomyiidae 5. <i>Stephomyia</i> cfr. <i>clavata</i> (Tavares, 1920) (Cecidomyiidae) 6. Cecidomyiidae	α -humulene; allo-aromadendrene; β -caryophyllene; β -selinene; γ -cadinene; α -cadinol; germacrene D; α -copaene; α -cubebene; α -muurolene; α -muurolol; aromadendrene; δ -cadinene	Amoebicide activity	Leaves and stem	Quercitrin	Apel <i>et al.</i> (2004); Bokesch <i>et al.</i> (2008); Zatelli (2015)
<i>Eugenia punicifolia</i> (Kunth) DC. / = <i>E. ovalifolia</i> Camb.	1. Cylindrical, green or reddish, glabrous, one-chambered. 2. Lenticular, green, glabrous, one-chambered. 3. Leaf Gall 4. Fusiform, brown, glabrous, multichambered. 5. Stem gall 6. Stem gall on stem. 7. Fruit, globoid, green or yellow, glabrous, multichambered. 8. Fruit gall	1. <i>Stephomyia</i> sp. (Cecidomyiidae) 2. Cecidomyiidae 3. Cecidomyiidae 4. Lasiopteridi (Diptera, Cecidomyiidae) 5. Hymenoptera 6. Undetermined 7. Undetermined 8. Cecidomyiidae	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; β -caryophyllene; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D; globulol; α -copaene; α -cubebene; α -muurolene; α -muurolol; limonene; viridiflorene; viridiflorol; linalool; aromadendrene; γ -elemene; δ -cadinene	Antioxidant activity	Leaves, stems, and fruits	Quercetin; quercitrin; myricetin; myricitrin; gallic acid;	Maia <i>et al.</i> (1997); Godoy <i>et al.</i> (1999); de Oliveira <i>et al.</i> (2005); Pereira <i>et al.</i> (2010); Ramos <i>et al.</i> (2010); Neves <i>et al.</i> (2024)



Table 1. Cont.

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Eugenia speciosa</i> Cambess. /-	1. Conical, yellow, glabrous, one-chambered 2. Claviform, green, glabrous, one-chambered	1. <i>Schizomyiina</i> (Cecidomyiidae) 2. <i>Schizomyiina</i> (Cecidomyiidae)	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; β -caryophyllene; globulol; limonene; viridiflorol; linalool; aromadendrene; δ -cadinene	-	Leaves	-	Alves et al. (2000); Apel et al. (2004)
<i>Eugenia sulcata</i> Spring ex Mart. /-	1. Bud, cylindrical, reddish, glabrous, one-chambered. 2. Bud, ovoid, green, glabrous. Galler: Undetermined	1. Undetermined 2. Undetermined	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; caryophyllene oxide; β -caryophyllene; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D; globulol; α -copaene; α -cubebene; limonene; viridiflorol; linalool	Antimicrobial activity	Leaves and buds	-	Apel et al. (2004) Ramos et al. (2010); Lima et al. (2012); da Silva et al. (2024)

Table 1. Cont.

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Eugenia uniflora</i> L. /-	1. Globoid, spongy, whitish, glabrous, one-chambered. 2. Conical, green or reddish, glabrous, one-chambered. 3. Lenticular, green, yellowish or black, glabrous, one-chambered. 4. Fruit, conical, reddish, glabrous, one-chambered. Galler: Cecidomyiidae 5. Conical, green, glabrous, one-chambered. 6. Bud flower, conical, reddish, glabrous, one-chambered. 7. Stem, fusiform, brown, glabrous, one-chambered. 8. Fold, green, glabrous, one-chambered.	1. <i>Maiamyia dispar</i> Maia, Mendonça & Romanovski, 1997, comb. nov. (<i>Eugeniamyia</i>) (Cecidomyiidae) 2. <i>Clinodiplosis profusa</i> Maia, 2001 (Cecidomyiidae) 3. <i>Neolasioptera eugeniae</i> Maia, 1993 (Cecidomyiidae) 4. Cecidomyiidae 5. <i>Maiamyia triangularis</i> Maia & Nava, 2011 comb. nov. (<i>Eugeniamyia</i>) (Cecidomyiidae) 6. Cecidomyiidae 7. Undetermined 8. Cecidomyiidae	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; caryophyllene oxide; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D; globulol; α -cubebene; limonene; viridiflorene; viridiflorol; linalool; aromadendrene; γ -elemene; δ -cadinene	Antimicrobial, antihyperglycemic, antypertriglyceridemia, anti-inflammatory, digestive, and hypotensive	Leaves, fruits, and stems	Quercetin; quercitrin; myricetin; myricitrin; gallic acid	Melo <i>et al.</i> (2007); Marin <i>et al.</i> (2008); Rodrigues <i>et al.</i> (2013); Santos <i>et al.</i> (2015); Mesquita <i>et al.</i> (2017); dos Santos <i>et al.</i> (2018); Silva TD <i>et al.</i> (2021);
<i>Myrcia amazonica</i> DC. /= <i>M. lundiana</i> Kiaersk	1. Globoid gall 2. Leaf gall 3. Bud ovoid, grooved. 4. Fusiform gall on flower peduncle 5. Leaf lenticular. 6. Leaf gall on vein.	1. <i>Dasineura</i> sp. (Cecidomyiidae) 2. Undetermined 3. <i>Myrciamyia maricaensis</i> Maia, 1995 (Cecidomyiidae) 4. Cecidomyiidae 5. Undetermined 6. Undetermined	α -pinene; β -pinene; α -terpineol; α -humulene; caryophyllene oxide; (E)-caryophyllene; β -selinene; α -selinene; limonene; linalool	Antifungal activity	Leaves	–	Alves <i>et al.</i> (2016); Melo <i>et al.</i> (2021)
<i>Myrcia brasiliensis</i> Kiaersk /= <i>Gomidesia schaueriana</i> O. Berg	1. Stem gall, fusiform, brown, glabrous, one-chambered. 2. Bud ovoid gall, multichambered, glabrous.	1. <i>Pacholenus pelliceus</i> Boheman, 1836 (Coleoptera: Curculionidae) 2. Undetermined	α -pinene; β -pinene; allo-aromadendrene; caryophyllene oxide; β -selinene; germacrene D; limonene; viridiflorol; γ -elemene	Antifungal activity	Leaves	–	Limberger <i>et al.</i> (2003); Pansera <i>et al.</i> (2021)



Table 1. Cont.

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Myrcia ovata</i> Cambess. /-	1. Globoid, yellow, glabrous, one-chambered. 2. Leaf gall 3. Ovoid, bud, green, grooved, glabrous, one-chambered. 4. Fusiform on flower peduncle, green, glabrous, one-chambered. 5. Conical, green, glabrous, one-chambered. 6. Conical, green, glabrous, one-chambered. 7. Marginal roll, green, glabrous, one-chambered. 8. Lenticular, green, glabrous, one-chambered.	1. <i>Dasineura</i> sp. (Cecidomyiidae) 2. Undetermined 3. <i>Myrciamyia maricaensis</i> Maia, 1995 (Cecidomyiidae) 4. Cecidomyiidae 5. <i>Dasineura</i> sp. (Cecidomyiidae) 6. Cecidomyiidae 7. Thysanoptera 8. Undetermined	α -pinene; β -pinene; α -terpineol; caryophyllene oxide; E-caryophyllene; β -selinene; α -selinene; linalool	Antibacterial, antibiofilm, fungicidal and anti-inflammatory activity	Leaves	–	Cândido <i>et al.</i> (2010); Lima <i>et al.</i> (2011); Jesus <i>et al.</i> (2016); Amorim <i>et al.</i> (2021)
<i>Myrcia palustris</i> DC. /= <i>Gomidesia palustris</i> (DS.) Kausel	1. Lenticular, green, glabrous, one-chambered. 2. Bud, ovoid gall, brown, glabrous, multichambered.	1. Undetermined 2. Undetermined	α -humulene; caryophyllene oxide; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D; globulol; α -copaene; α -cubebene; α -muurolene; viridiflorene; aromadendrene; δ -cadinene	Formicidal and antimicrobial	Leaves	–	Limberger <i>et al.</i> (2003); Santos <i>et al.</i> (2021)

Table 1. Cont.

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Myrcia splendens</i> (SW.) DC. / = <i>M. fallax</i> (Rich.) DC.	1. Globoid, green, glabrous, one-chambered. 2. Conical, yellow or green, glabrous, one-chambered. 3. Marginal roll, green, glabrous, one-chambered. 4. Leaf roll, reddish, glabrous, one-chambered. 5. Bud globose, green or brown, glabrous, multichambered. 6. Globoid, brown, glabrous. 7. Globoid, brown, glabrous, one-chambered. 8. Bud gall. 9. Stem, fusiform, multichambered. 10. Stem or leaf vein. 11. Bud conical.	1. Undetermined 2. Undetermined 3. Undetermined 4. Undetermined 5. Undetermined 6. Lasiopteridi (Cecidomyiidae) 7. Lasiopteridi (Cecidomyiidae) 8. Lasiopteridi (Cecidomyiidae) 9. Cecidomyiidae 10. Lasiopteridi (Cecidomyiidae) 11. Undetermined	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; caryophyllene oxide; β -caryophyllene; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D; globulol; α -copaene; α -cubebene; α -muurolene; α -muurolol; limonene; viridiflorene; viridiflorol; linalool; aromadendrene; γ -elemene; δ -cadinene	Antioxidant and antifungal activity	Leaves	Quercitrin; myricitrin; myricetin; gallic acid	Cole <i>et al.</i> (2008); Nakamura <i>et al.</i> (2010); Pereira <i>et al.</i> (2010); Guldbrandsen <i>et al.</i> (2014); Jorge <i>et al.</i> (2018); Montalvão <i>et al.</i> (2023)
<i>Myrciaria floribunda</i> (West ex Willdenow) Berg /-	1. Globoid, green, glabrous, one-chambered. 2. Conical, yellow or green, glabrous, one-chambered. 3. Marginal roll, green, glabrous, one-chambered. 4. Leaf roll, reddish, glabrous, one-chambered. 5. Globoid, green or brown, glabrous, multichambered. 6. Globoid, brown, glabrous.	1. Undetermined 2. Undetermined 3. Undetermined 4. Undetermined 5. Undetermined 6. Lasiopteridi (Cecidomyiidae) 7. Lasiopteridi (Cecidomyiidae) 8. Lasiopteridi (Cecidomyiidae)	α -pinene; α -terpineol; α -humulene; allo-aromadendrene; E-caryophyllene; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D;	Anti-inflammatory activity	Leaves and fruits	Gallic acid	Ramos <i>et al.</i> (2010); de Oliveira <i>et al.</i> (2018); García <i>et al.</i> (2021); García <i>et al.</i> (2022); Dos Santos de Moraes <i>et al.</i> (2023);



Table 1. Cont.

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Myrciaria floribunda</i> (West ex Willdenow) Berg /-	7. Globoid brown, glabrous, one-chambered. 8. Gall on bud. 9. Stem, fusiform, multichambered. 10. Stem or leaf vein. 11. Bud, conical.	9. Cecidomyiidae 10. Lasiopteridi (Cecidomyiidae) 11. Undetermined	globulol; α -copaene; α -cubebene; α -muurolene; α -muurolol; viridiflorene; viridiflorol; aromadendrene; γ -elemene; δ -cadinene				
<i>Neomitranthes obscura</i> (DC.) N. Silveira /-	1. Conical, green, glabrous, one-chambered. 2. Leaf roll, green, glabrous, one-chambered. 3. Fusiform, green, glabrous, one-chambered. 4. Roll marginal, green, glabrous, one-chambered. 5. Pineapple-shaped, green, glabrous. 6. Fusiform, brown, glabrous, one-chambered.	1. Cecidomyiidae 2. <i>Thysanoptera</i> 3. <i>Stephomyia mina</i> Maia, 1993 (Cecidomyiidae) 4. <i>Clinodiplosis</i> sp. (Cecidomyiidae) 5. <i>Neomitranthella robusta</i> Maia, 1995 (Cecidomyiidae) 6. Undetermined	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; caryophyllene oxide; E-caryophyllene; β -selinene; α -selinene; γ -cadinene; α -cadinol; germacrene D; globulol; α -copaene; α -cubebene; α -muurolene; α -muurolol; limonene; linalool; aromadendrene; γ -elemene; δ -cadinene	-	Leaves, stem, and fruits	Delphinidin-3-O-glucoside; cyanidin-3-O-glucoside	Ramos et al. (2010); Amaral et al. (2013); Gouvêa et al. (2015); Victório et al. (2018)

Table 1. Cont.

Plant Species/Synonyms	Gall morphotypes according to Maia VC (2019)	Inducers	Most abundant monoterpenes and sesquiterpenes	Biological activity	Organ	Most abundant phenolic compounds	References
<i>Plinia peruviana</i> (Poir.) Govaerts /= <i>P. cauliflora</i> (Mart.) Kausel, <i>Myrciaria jaboticaba</i> (Vell.) O. Berg	1. Marginal roll, green, glabrous, one-chambered. 2. Cylindrical, green, glabrous, one-chambered.	1. Cecidomyiidae 2. Cecidomyiidae	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; caryophyllene oxide; β -caryophyllene; α -cubebene; linalool; aromadendrene; δ -cadinene	Healing and antioxidant activity	Leaves and fruits	Quercetin; quercitrin; myricetin; myricitrin; gallic acid; delphinidin-3-glucoside; cyanidin-3-O-glucoside;	da Silva <i>et al.</i> (2019); Inada <i>et al.</i> (2018); Almeida <i>et al.</i> (2025)
<i>Psidium cattleyanum</i> Sabine /= <i>P. cattleianum</i> Sabine	1. Biconical, green, glabrous, one-chambered. 2. Globoid, yellow, glabrous, one-chambered. 3. Fusiform, brown, glabrous, multichambered. 4. Tubular, green, glabrous, one-chambered. 5. Rosette green, glabrous. 6. Conical, with small apical projections, green, glabrous. 7. Globoid, one-chambered. 8. Lenticular.	1. <i>Tectococcus ovatus</i> Hempel (Eriococcidae, Hemiptera) 2. Cecidomyiidae 3. Undetermined 4. Lasiopteridi (Cecidomyiidae) 5. <i>Dasineura gigantea</i> Angelo & Maia, 1999 (Cecidomyiidae) 6. Cecidomyiidae 7. Undetermined 8. Cecidomyiidae	α -pinene; β -pinene; α -terpineol; α -humulene; allo-aromadendrene; caryophyllene oxide; β -caryophyllene; β -selinene; α -selinene; γ -cadinene; α -cadinol; globulol; α -copaene; α -muurolene; α -muurolol; limonene; viridiflorol; linalool; aromadendrene; δ -cadinene	Anti-inflammatory and antioxidant activity	Leaves, stems, and buds	Quercetin; quercitrin; myricetin; gallic acid; cyanidin-3-O-glucoside	Marin <i>et al.</i> (2008); Adam <i>et al.</i> (2011); Silva TD <i>et al.</i> (2021); El-Deeb <i>et al.</i> (2024)



patterns of the most abundant volatile compounds, a presence/absence matrix was generated. Regarding the distribution of total volatile compounds, the data were quantified and characterized into chemical subclasses. A heatmap was generated using the *vegan* (Oksanen *et al.*, 2022) and *pheatmap* (Kolde, 2019) packages in R Studio (Posit Team, 2025).

For phenolic compounds, we performed a histochemical analysis of metabolite distribution on leaves, non-galled buds, and mature galls induced on *N. obscura* by the following Cecidomyiidae (Diptera): the marginal leaf-rolling galls induced by *Dasineura tavaresi* Maia, 1995; the clavate and lenticular leaf galls induced by unidentified cecidomyiids, and rosette galls induced on buds by *Neomitranthella robusta* Maia, 1995 (Maia, 2024). Samples of ungalled organs and galls (n = 5) were collected in the Maricá *restinga*, Rio de Janeiro state, Brazil (22°57'39.1" S; 42°50'45.8" W). The samples were fixed in 2.5 % glutaraldehyde and 4.5 % formaldehyde in 0.1 M phosphate buffer, pH 7.2 (Karnovsky, 1965) and sectioned using razor blades and submitted to 10 % ferric chloride for 5 minutes (Johansen, 1940). The slides were mounted in distilled water, observed, and photographed under a light microscope (Leica® DM2500) with a coupled digital camera (Leica® DFC7000 T).

Results

The most abundant chemical compounds per species

Thinking about the extremes in terms of gall morphotypes, the 16 species of Myrtaceae that serve as superhosts for galling herbivores are rich in secondary metabolites (Table 1), with sesquiterpene hydrocarbons as the major chemical class. Among these chemical subclasses, the β -selinene was the most common chemical compound, reported for 13 species. The distribution of the other most abundant compounds among the species is shown in Figure 2.

The diversity of chemical subclasses

The chemical compounds of the Myrtaceae are distributed into monoterpene hydrocarbons (MH), oxygenated monoterpenes (OM), sesquiterpene hydrocarbons (SH), and oxygenated sesquiterpenes (OS) (Table 2). Regarding the richness distribution among the chemical subclasses, *M. brasiliensis* (3.81), *E. copacabanensis* (3.71), *E. astringens* (3.68), and *E. speciosa* (3.61) have a well-distributed chemical profile (DV > 3.6). *Eugenia hiemalis* (2.17) and *M. palustris* (2.22)

Table 2. Distribution of chemical compounds among monoterpene hydrocarbons (MH), oxygenated monoterpenes (OM), sesquiterpene hydrocarbons (SH), and oxygenated sesquiterpenes (OS).

Species	Richness (Total terpenes)	Proportion in % of terpene classes				DCQ	DV
		MH	OM	SH	OS		
<i>Eugenia astringens</i>	110	17 (15.4 %)	15 (13.6 %)	44 (40 %)	34 (31 %)	1.30	3.68
<i>Eugenia copacabanensis</i>	53	4 (7.5 %)	17 (32 %)	15 (28.3 %)	17 (32 %)	1.31	3.71
<i>Eugenia hiemalis</i>	46	1 (2.1 %)	0 (0 %)	28 (60.8 %)	17 (37 %)	0.78	2.17
<i>Eugenia puniceifolia</i>	95	14 (14.7 %)	8 (8.4 %)	48 (50.5 %)	25 (26.3 %)	1.20	3.33
<i>Eugenia speciosa</i>	59	25 (42.3 %)	6 (10.1 %)	18 (30.5 %)	10 (17 %)	1.29	3.61
<i>Eugenia sulcata</i>	64	10 (15.6 %)	4 (6.25 %)	26 (40.6 %)	24 (37.5 %)	1.22	3.39
<i>Eugenia uniflora</i>	70	8 (11.4 %)	2 (2.8 %)	30 (42.8 %)	30 (42.8 %)	1.10	3.00
<i>Myrcia amazonica</i>	45	10 (22.2 %)	26 (57.7 %)	5 (11.1 %)	4 (8.8 %)	1.14	3.14
<i>Myrcia brasiliensis</i>	56	6 (10.7 %)	14 (25 %)	20 (35.7 %)	16 (28.5 %)	1.34	3.81
<i>Myrcia ovata</i>	30	3 (10 %)	17 (56.6 %)	4 (13.3 %)	6 (20 %)	1.19	3.30
<i>Myrcia palustris</i>	45	1 (2.2 %)	0 (0 %)	25 (55.5 %)	19 (42.2 %)	0.80	2.22
<i>Myrcia splendens</i>	80	7 (8.7 %)	7 (8.7 %)	39 (48.7 %)	27 (33.7 %)	1.16	3.20
<i>Myrciaria floribunda</i>	120	17 (14.1 %)	23 (19.1 %)	60 (50 %)	20 (16.67 %)	1.25	3.49
<i>Neomitranthes obscura</i>	102	8 (7.8 %)	14 (13.7 %)	45 (44.1 %)	35 (34.3 %)	1.22	3.37
<i>Plinia peruviana</i>	21	6 (28.5 %)	3 (14.2 %)	11 (52.3 %)	1 (4.7 %)	1.19	3.29
<i>Psidium cattleianum</i>	64	12 (18.7 %)	6 (9.3 %)	29 (45.3 %)	17 (26.5 %)	1.25	3.48

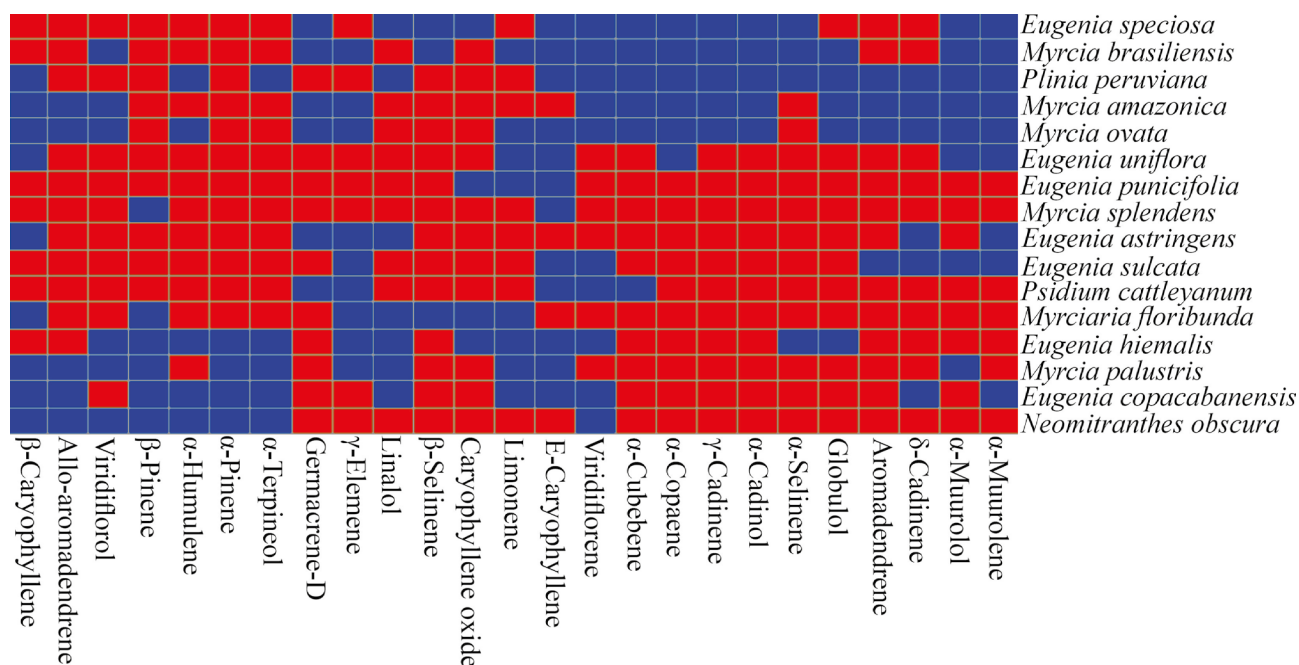


Figure 2. Absence and presence matrix of the most abundant chemical compounds per species. Red indicates presence; Blue indicates absence.

have the lowest distribution of compounds among the chemical subclasses (DV < 3). Regarding the highest percentages of chemical compounds in each class, *E. speciosa* has 42.3 % of MH, *M. ovata* has 56.6 % of OM, *E. hiemalis* has 60.8 % of SH, and *E. uniflora* has 42.8 % of OS. Regarding the lowest percentages of compounds per chemical class, *E. hiemalis* has 2.1 % of SH. *Eugenia hiemalis* and *M. palustris* have no OM, *M. amazonica* has 11.1 % of SH, and *P. peruviana* has 4.7 % of OS.

The heatmap revealed clear patterns in the abundance of chemical compounds per subclass among species. *Eugenia astringens*, *E. punicifolia*, *M. floribunda*, and *N. obscura* showed the highest variation and overall abundance in SH. The MH showed moderate abundance, with *E. astringens*, *E. speciosa*, and *M. floribunda* standing out among the group. The OS revealed intermediate variation, with higher values concentrated in *E. astringens* and *N. obscura*. In contrast, the OM exhibited consistently low values among most species, with a slight increase observed in *M. amazonica* (Fig. 3).

The case study of *Neomitranthes obscura*

Neomitranthes obscura has the third richest terpenoid profile among the 16 superhost Myrtaceae species analyzed herein, due to its diversity of hydrocarbon and oxygenated sesquiterpenes, sharing β-selinene, α-selinene, caryophyllene oxide, aromadendrene, γ-cadinene, α-cadinol, globulol, α-copaene, germacrene D, α-cubebene, δ-cadinene, α-murolol, limonene, α-murolene, γ-elementene, and E-caryophyllene with the other species. However, seven compounds found in other Myrtaceae species have not

been reported for *N. obscura*; these include α-pinene, β-pinene, α-humulene, α-terpineol, viridiflorol, linalool, and viridiflorene.

Regarding the phenolic compounds, the literature data indicate the chemical affinity of *N. obscura* to *Plinia peruviana*, which also contains delphinidin-3-O-glucoside. For *Psidium cattleianum*, both the sharing of cyanidin 3-O-glucoside and delphinidin-3-O-glucoside indicate higher chemical similarity. Nevertheless, the sesquiterpene profile of these three species is diverse, except for the SH. (Table 1). Additionally, *N. obscura* gall morphotypes show total phenolic compounds predominantly concentrated in the outer compartment tissues, while for the other host Myrtaceae species, the phenolics were detected all over gall tissues (Fig. 4).

Discussion

The analysis of the terpenoid profile of the studied species, based on literature data, indicated high heterogeneity. However, some compounds are shared by most of the species, indicating a certain affinity among them, such as *E. astringens*, *E. uniflora*, and *P. cattleianum*, which demonstrates the richer diversity of volatile compounds in our survey. In Rio de Janeiro state, the superhosts of *restingas* with the highest number of distinct gall morphotypes reported are *E. uniflora* and *E. astringens* (Martins *et al.*, 2023), whose diversity of terpenoids includes limonene, E-caryophyllene, and γ-cadinene. The sesquiterpene hydrocarbon (E)-caryophyllene, for example, has even been



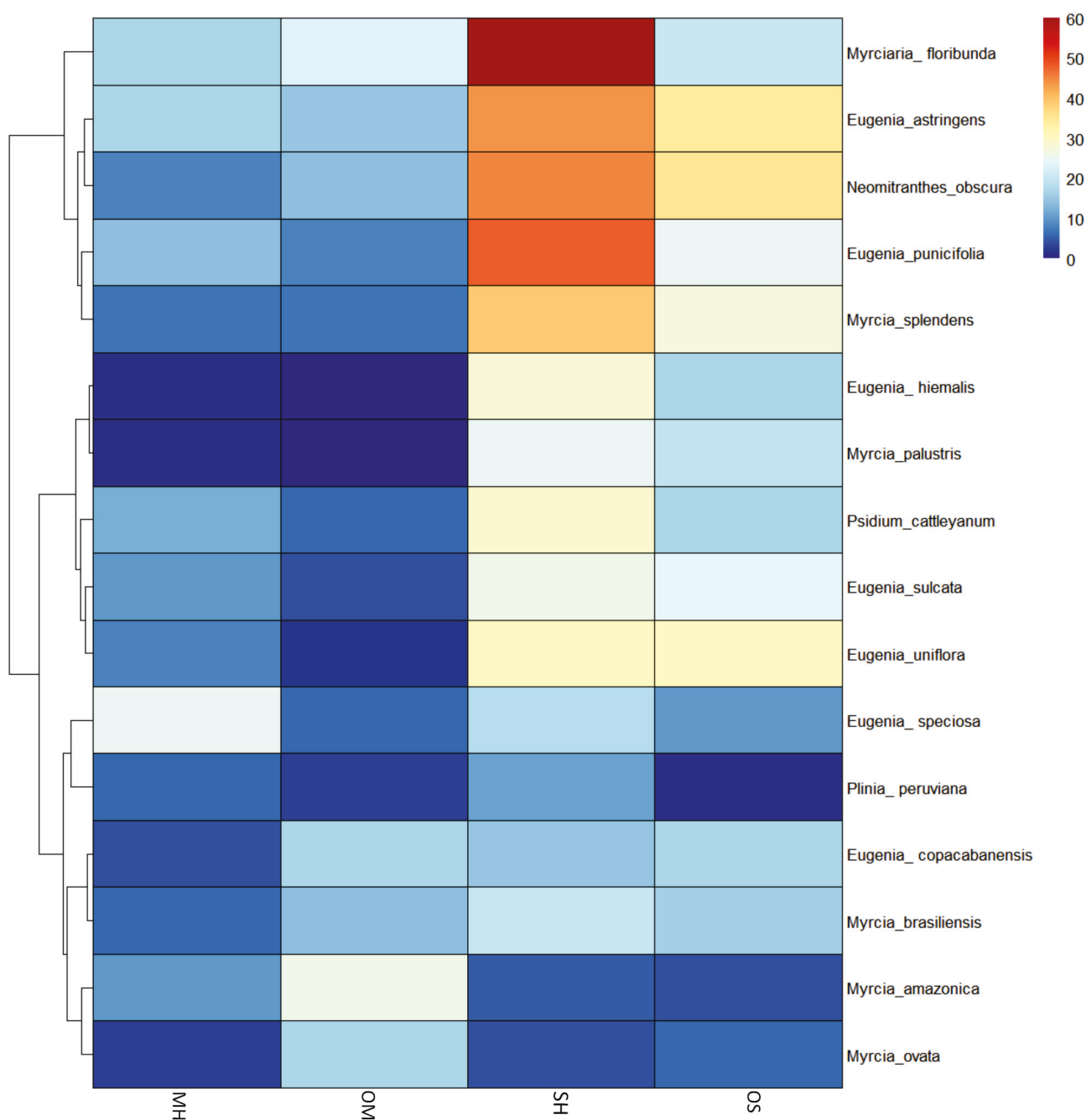


Figure 3. Distribution of chemical subclasses on Myrtaceae species. The heatmap illustrates the distribution of four classes: monoterpene hydrocarbons (MH), oxygenated monoterpenes (OM), sesquiterpene hydrocarbons (SH), and oxygenated sesquiterpenes (OS). Color key indicates chemical class expression value, blue: lowest, red: highest.

associated with stimulating the oviposition of *Orseolia oryzivora* (Cecidomyiidae) on *Oryza sativa* plants (Ogah et al., 2017). Among the monoterpenes, alpha-pinene, beta-pinene, and limonene can be mentioned, which are involved in the attraction and oviposition of females of *Antistrophus rufus* (Hymenoptera) on *Silphium* (Asteraceae) (Tooker et al., 2005), and increased γ -terpinene and α -pinene in *Eucalyptus* trees are also associated with the susceptibility of plants to *Leptocybe invasa* Fisher & La Salle (Hymenoptera) infestations

(Naidoo et al., 2018). On the other hand, the γ -cadinene is an early enzymatic intermediate in the biosynthesis of sesquiterpene phytoalexins (Tholl, 2015), and if these phytoalexins accumulate in the tissues of the hosts, this may activate the defense system, leading to hypersensitive responses and avoiding gall development (Fernandes, 1990). Besides that, the functions and mechanisms of action of phytoalexins are relatively unknown (Ahuja et al., 2012), but some galls, like those induced on the *Parrotia subaequalis*

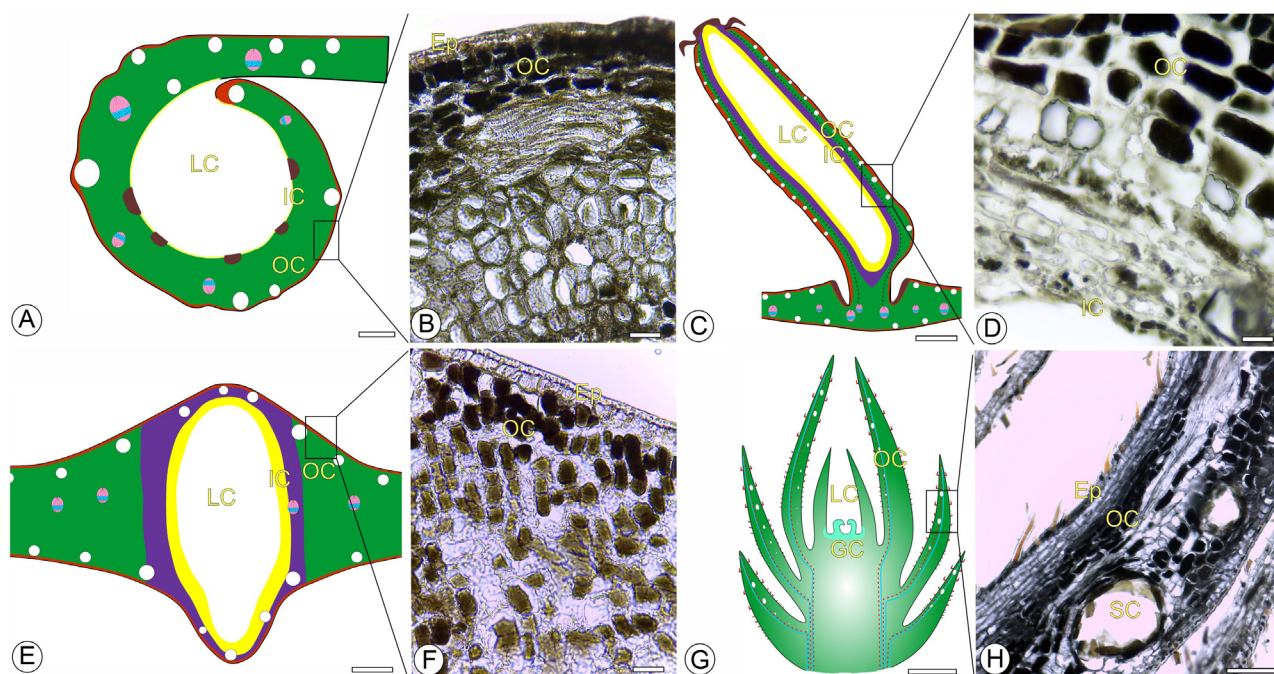


Figure 4. Histolocalization of phenolic compounds on *Neomitrantbes obscura* (DC.) N. Silveira. **A-B** Marginal rolling gall. **A.** Diagram of the gall in transverse section. **B.** Detection of phenolic compounds on outer tissue compartment. **C-D.** Clavate gall. **C.** Diagram of the gall in transverse section. **D.** Concentration of phenolic compounds in the vacuole of outer tissue compartment layers. **E-F.** Lenticular gall. **E.** Diagram of the gall on transverse section, evidencing tissue organization. **F.** Detection of phenolic compounds on mesophyll layers. **G-H.** Bud gall. **G.** Diagram of the gall evidencing leaf primordia and leaf projections. **H.** Gall homogenous parenchyma with an accumulation of phenolics. (Ep=Epidermis; GC=Gall Core; IC=Inner Compartment; LC=Larval Chamber; OC=Outer Compartment; SC=Secretory Cavity). Scale bars: 500µm(G), 200µm (A, E), 50µm (B, D, H).

(H.T. Chang) R. M. Hao et H. T. Wei (Hamamelidaceae), accumulate different types of phytoalexins (Zhou *et al.*, 2025), indicating a possible role of these compounds in the establishment of galling species-host plant associations.

Despite belonging to distinct phylogenetic lineages (*sensu* Vasconcelos *et al.*, 2015), *N. obscura* exhibits a strong chemical similarity with *Plinia peruviana*, which may reflect convergent adaptive strategies or the conservation of biochemical traits within the tribe Myrteae (Padovan *et al.*, 2014). Notably, *E. astringens*, the species with the most diverse terpenoid profile, is one of the species with the most associated galls among Myrtaceae superhosts, with at least six galling insects associated, among those reported to Rio de Janeiro State (Martins *et al.*, 2023). When we compared the association species-terpenoid profile, we can observe a tendency toward diversity in the terpenoid profile (expressed in SH and OS), especially in superhost species (Fig. 3) when compared to the other species, except for *M. ovata* and *E. copacabanensis*. Therefore, we can associate the diversity of terpenoids types with the richness of associated gall inducers. The metabolic diversity of the superhosts may indicate that they are more able to respond to biotic interactions, possibly altering their biochemical pathways, which is yet to be explored.

One of the most common chemical compounds, β -selinene, which is reported in most species, is known for its allelopathic effects (Bewick *et al.*, 1994). Recently, the joint effects of herbivory and allelopathy on driving the diversity-invasibility relationship were proposed in a 2-year experiment, providing a perspective for future studies (Wang *et al.*, 2025). Beyond its allelopathic potential, β -selinene-derived products are associated with defense-promoting mechanisms in model plants, like maize, against fungi and some insects (Ding *et al.*, 2017); however, they may also act in the attraction of plant-parasitic nematodes (Ali *et al.*, 2011). In our review, we have not found the occurrence of galls induced by nematodes in the Myrtaceae species; however the preponderance of β -selinene in most superhosts may indicate the occurrence of trade-offs between plant defense and herbivore attraction by this chemical group, in a similar way as the DIMBOA metabolites in grasses, which were previously indicated as a potential mechanism to understand host-galler associations (Arriola *et al.*, 2024). It is reinforced by its relationship with smell emissions by some insects (Sakurai *et al.*, 2020). Other chemical compounds like β -pinene, α -terpineol, allo-aromadendrene, γ -cadinene, α -cadinol, and globulol are very common in the superhost Myrtaceae analyzed herein, despite their insect repellent effects (Mya *et al.*, 2017). The α -terpineol and



alloaromadendrene exhibit antioxidant effects (Chen *et al.*, 2023; Yu *et al.*, 2014), which may mitigate the impact of excess reactive oxygen species commonly found in the gall tissue environment, resulting from the high metabolism of the galling larvae and plant cells. Such compounds may be of metabolic interest for the superhost Myrtaceae and other taxa associated with several gall-inducing species, which have yet to be evaluated.

Regarding the volatile components, chemical data revealed the prevalence of non-oxygenated terpenoids, with a greater diversity among sesquiterpenes, which can be chemotaxonomic markers for these superhost taxa within the Myrtaceae. The sesquiterpenes tend to be semivolatile due to oxygenation. From a biological activity perspective, the low oxygenation of the components of the mono- and sesquiterpenes is related to their high volatility. Volatile terpenoids possess a series of signaling properties whose role in host selection has been observed in insects, including those from galling taxonomic groups. There is still little research on the importance of terpenoids in attracting gall inducers. These metabolites may play a key role in host plant selection by gall inducers (Tooker *et al.*, 2008).

Although phenolics are highly important in host plant-galling insect systems, few studies on the superhost Myrtaceae have isolated such a group of chemical compounds. The histochemical analysis of non-galled and galls on *N. obscura* confirmed the intense accumulation of phenolic compounds. In general, these phenolic metabolites, such as simple derivatives (gallic acid and cinnamic acids), gallic and condensed tannins, and monomeric flavonoids, play a key role in redox balance, which may favor galler establishment (Ferreira *et al.*, 2018; Guedes *et al.*, 2019; 2022). However, the data presented here do not reveal any discernible patterns related to superhosts. Future studies could compare host and non-host Myrtaceae species in *restingas* to assess whether superhosts exhibit quantitative or qualitative differences in phenolic compounds.

The metabolite profile of Myrtaceae superhosts reveals chemotaxonomic similarities, yet no obvious pattern fully explains their role as gall superhosts. Several Myrtaceae superhosts possess a wide range of hydrogenated sesquiterpenes and oxygenated sesquiterpenes, differentiating them from other hosts, although this is not a rule. Many of the substances produced by Myrtaceae superhosts, particularly mono- and sesquiterpenoids, may function as chemical signals for gall-inducing herbivores. The fact that these plants are related and emit chemically similar volatile signals may provide clues to unraveling the mystery of superhosts. Further chemoeological studies involving the effects of specific volatile signal emissions on galling species of these Myrtaceae are needed. A remaining question is why certain Myrtaceae species host diverse galling herbivores while closely related species do not? To address this, further chemical studies should investigate how specific volatile emissions influence galling insect preferences and colonization in these plants.

Acknowledgments

The authors thank the Researchers of the “Structure, Physiology and Chemistry of Neotropical Galls” team for field support and scientific discussions that enriched the final version of the manuscript.

Authors' Contributions

MAMR and CVCG: conceptualization, data curation, formal analysis, methodology, visualization, writing – original draft, review and editing; ÍAA and GLGS: formal analysis, writing – original draft, review and editing; RMSI and BGF: conceptualization, supervision, funding acquisition, project administration, resources, writing – review and editing.

Conflicts of Interest

The authors declare that there are no conflicts of interest.

Data Availability

All data supporting the findings of this study are included in the article.

Funding Information

The authors thank Fundação de Amparo à Pesquisa do Estado de Minas Gerais (FAPEMIG) for financial support, scholarship to MAMR and postdoctoral fellowship to ÍAA (RED-00039-23), Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for RMSI (309713/2023-4) and BGF (310520/2023-1) scholarships and grants, and Fundação de Amparo à Pesquisa do Estado do Rio de Janeiro (FAPERJ) for project support to BGF (E-26/204.608/2024; E-26/210.586/2025).

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